OBSERVATIONS ON THE HEART IN THE FAMILY TRIONYCHIDAE

BY

SABET GIRGIS, Ph.D. (Lond.)

University of Khartoum

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OBSERVATIONS ON THE HEART IN THE FAMILY TRIONYCHIDAE

By SABET GIRGIS, Ph.D. (Lond.)

SYNOPSIS

In the family TRIONYCHIDAE the heart is asymmetrically situated in the right side of the body cavity, lateral to the base of the neck, and is tilted so that its mid-longitudinal axis forms an an acute angle (approximately 45°) with the sagittal axis of the body. This hitherto unrecorded characteristic of the family has been shown by dissection of specimens representing its different genera. The position of the heart is due to two combined factors : (*a*) the retractility of the head and neck within the carapace, and (*b*) the reduction of the dorso-ventral axis of the body so that the carapace and plastron lie near each other, the former being only slightly convex. The tilting of the heart occurs later in life as it is not seen in new hatches, and it may be due to a pulling force exerted by the left arterial arches.

The anatomical structure of the heart of *Trionyx triunguis* is given. Comparison with *Cyclanorbis oligotylus* shows in the latter a prominent dorso-ventral *secondary septum* which divides the posterior part of the cavum magnum (dorsale) of the ventricle into right and left parts, while the septum in *Trionyx* is quite short.

Distribution of blood into the arterial arches, based purely on anatomical features, is as follows : (*a*) oxygenated blood into the right aorta, (*b*) mixed blood into the left aorta and (c) deoxygenated blood into the pulmonary arch. Blood analysis in the three vessels and in the right and left auricles, agrees with the anatomical findings.

INTRODUCTION

(a) *General*

THE heart of the Trionychidae is in many respects similar to that of other Chelonians as described by several authors including Bojanus (1819–21), Rathke (1848), Fritsch (1869), Huxley (1871), Hoffmann (1882), Greil (1903), Burne (1905), O'Donoghue (1918), Goodrich (1919), Thomson (1932), Hyman (1939), Ashley (1955) and others.

Contraction of the heart received the attention of many workers, especially as regards the nerve elements, the cardiac muscles and the route of the contraction wave. A comprehensive review on heart contraction in poikilothermal and homiothermal vertebrates is given by Davies & Francis (1945).

The double circulation through the heart of Chelonians and other reptiles was tackled by practically all the workers who described the anatomy, and most of them have reasoned from the anatomic relations of the cardiac cavities and vessels rather than from experimental evidence. The following papers on circulation are of special interest : Foxon (1955) ; von Hofsten (1941) ; Ewer (1950) ; Foxon, Griffith & Price (1953) ; Stephen (1954) ; and Steggerda & Essex (1957).

(b) *Position of Heart*

The peculiar asymmetric position of the heart in the antero-right side of the body cavity, and the tilting of the heart so that its mid-longitudinal axis forms an acute angle with that of the body as a whole are interesting, common characteristics of all members of the Trionychidae, hitherto unrecorded except for one of its members, the Indian mud turtle *Lissemys punctata* Kaushiva (1940), Mathur (1946), Ahsan Al-Islam & Iftikhar Hamid (1951) and Dhillon (1938).

During the course of this work the striking position and tilting of the heart were noticed in the common Nile turtle *Trionyx triunguis* and *Cyclanorbis oligotilus*, which is rather rare in the vicinity of Khartoum (but quite common in the Southern Sudan). It was then interesting to find out whether these characteristics were also shared by other members of the family Trionychidae. The answer was only made possible by the extreme kindness and co-operation of the Keeper of Zoology and of the Staff of the Herpetology Section of the British Museum (Natural History) London. As a guest of the Department during May and June, 1960, the writer was allowed to examine a fairly large number of alcohol-preserved specimens collected from various parts of the world, one and all of which had their hearts at the right side of the base of the neck and tilted to a degree which showed some variation in different species.

Based mainly on the Museum material examined, the two species of the Nile, the work published on the Indian mud turtle and two new hatches of *Amyda ferox spinifera* presented to the author by a friend in America, an important conclusion regarding the position of the heart in the Trionychidae could be arrived at and the relationship between this anatomical feature to the aquatic life of its members discussed.

(c) *Anatomy of Heart*

Trionyx triunguis being available in any required number, was chosen for a study of the anatomy of the heart, the great veins, the arterial arches, the heart beat and the double circulation. A comparative study of the heart of *Cyclanorbis oligotylus* followed.

(d) *Experimental*

Steggerda & Essex (1957) in *Chelydra serpentina*, state that " the saturation levels of the blood leaving the heart via the right and left aortas are the same while pulmonary artery blood is distinctly more venous ". This statement disagrees with the findings of the present work (based merely on anatomical features), where the right aorta carries blood with a distinctly higher oxygen saturation than the left, and it was therefore found necessary to perform a series of blood analysis tests of samples taken from the two aortae and the pulmonary artery, as well as from the left and right auricles, to verify this point.

(e) *Materials and Methods*

Specimens were caught by local fishermen from both the Blue Nile and the White Nile, as well as from Gebel Auleia Dam on the White Nile (25 miles south of Khartoum).

Animals were killed by injecting 5 c.c. of chloroform intramuscularly and setting them free to run vigorously and die in 10–15 minutes. For blood-analysis, specimens of exceptionally large sizes were chosen as 25 c.c. of blood had to be drawn from each; 3 c.c. of chloroform were injected in each specimen and it took 30–40 minutes, and occasionally longer, for an animal to lie unconscious.

ASYMMETRICAL POSITION OF THE TRIONYCHID HEART

The following examples are meant to cover all the known genera of the family Trionychidae. Numbers 2, 4, 5, 6, 7, 8 and 10 are alcohol-preserved specimens from the British Museum (Natural History), London.

In each case the plastron is removed to expose the ventral body wall and the two great triangular masses of pectoral muscles. The heart lies for the most part dorsal to the right mass, and to expose it the muscular and fibrous tissues which extend between the pectoral muscles on the one hand and the neck and ventral wall of the abdomen on the other hand, have to be carefully severed. The ventral wall of the pericardium is now cut off and the pericardial cavity, the heart (in ventral view) and the arterial arches are exposed (Text-fig. 1).

The pericardial cavity containing the heart lies roughly dorsal to the right mass of the pectoral muscles, ventral to the concave antero-lateral surface of the right liver lobe, anterior to the bulk of the right liver lobe and posterior to the postero-right part of the base of the neck (Text-fig. 1).

1. ***Trionyx triunguis.*** Locality Khartoum, Sudan.

Six specimens were chosen, the smallest weighed 1,370 g. and the dimensions of its carapace were 26 × 23 cm.; and the largest weight 14,320 g. and its carapace was 50 × 46 cm.

The heart lies at the anterior part of the body cavity, some distance to the right of the mid-longitudinal axis of the body. The mid-longitudinal axis of the heart, taken as the line perpendicular on the transverse axis of the ventricle at its medial point, forms an acute angle with the mid-longitudinal axis of the body. The angle averaged 45° in the six specimens.

2. ***Trionyx triunguis.*** (B.M. 87.3.2.8–12, 13; from the Lower Congo.)

A very young specimen, much smaller than any examples in our local (Khartoum) collection.

Weight of specimen = 11·2 g.
Dimensions of carapace = 5·2 × 4·4 cm.

The heart was in the same position as in the older specimens and tilted to the same degree.

3. ***Cyclanorbis oligotylus.*** Locality Khartoum, Sudan.

Six specimens of a fairly large size were examined. The smallest weighed 4,150 g. and the dimensions of its carapace were 24 × 22·5 cm.

The heart was in every case at the antero-right side of the body cavity but nearer to the sagittal plane than in any other Trionychid. The mid-longitudinal axis

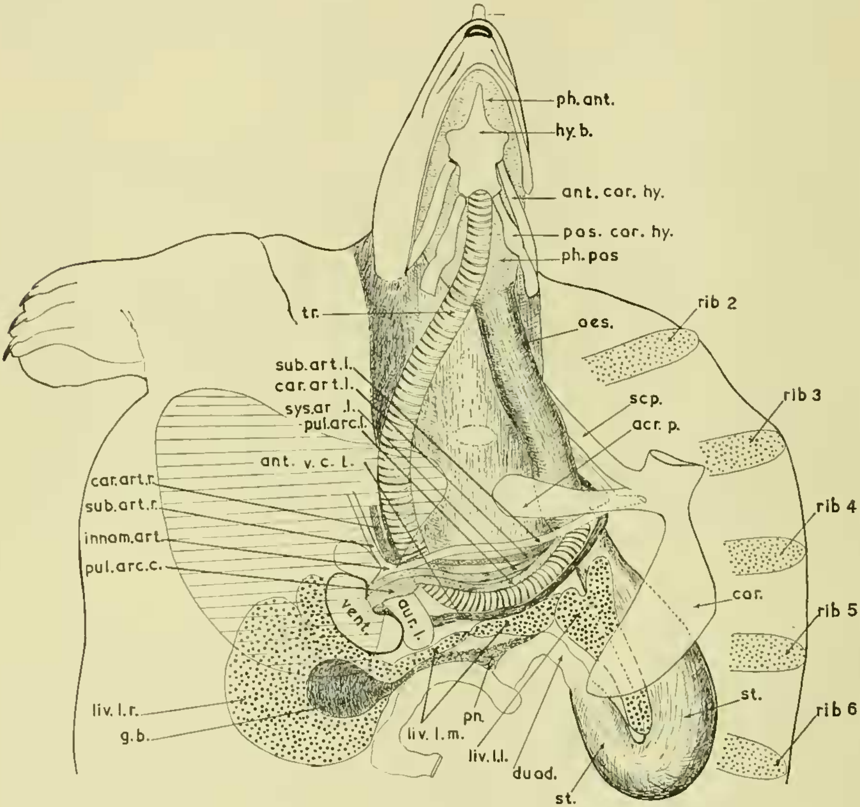

FIG. 1. *T. triunguis.* Dissection to show the position of the heart in relation to other parts of the body.

acr. p., acromal process ; ant. cor. hy., anterior cornu of hyoid ; ant. v. c. l., left anterior vena cava ; car. art. l., left carotid artery ; car. art. r., right carotid artery ; cor., coracoid bone ; duod., duodenum ; g. b., gall bladder ; hy. b., hyoid body ; innom. art., innominate artery ; liv. l. l., left liver lobe ; liv. l. m., medial liver lobe ; liv. l. r., right liver lobe ; oes., oesophagus ; ph. ant., anterior pharynx ; ph. post., posterior pharynx ; pn., pancreas ; pos. cor. hy., posterior cornu of hyoid ; pul. arc. c., common pulmonary arch ; pul. arc. l., left pulmonary arch ; pyl. sp., pyloric sphincter ; scp., scapula ; st., stomach ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sys. arc. l., left systemic arch ; tr., trachea.

of the body passed through the left side of the left auricle. The tilting of the heart was comparable to *Trionyx*.

4. ***Cycloderma frenatum.*** (B.M. 1945.1.1.1–5 ; from Fort Johnson, Nyasaland.)

Weight of specimen = 14·7 g.
Dimensions of carapace = 4·8 × 3·6 cm.

The heart was in the same position as in *Trionyx*, but tilted to a lesser extent. Its mid-longitudinal axis formed an angle of approximately 35° with the mid-longitudinal axis of the body.

5. ***Pelochelys bibroni.*** (B.M. 1921.11.11.4 ; from Wangar River, Dutch New Guinea.)

Weight of specimen = 122·7 g.
Dimensions of carapace = 10·6 × 10·2 cm.

The heart was in the same position as in *Trionyx*, and the amount of tilting as in the previous specimen of *Cycloderma*.

6. ***Dogania subplana.*** (B.M. 93.3.6.9–11, from Sarawak, Borneo.)

Weight of specimen = 66·3 g.
Dimensions of carapace = 9·2 × 7·3 cm.

The heart was exactly as in *Trionyx* as regards position and tilting.

7. ***Lissemys punctata.*** (B.M. 84.3.25.3 ; from unknown locality, somewhere in India.)

A very young specimen.

Weight of specimen = 8·2 g.
Dimensions of carapace = 3·3 × 2·7 cm.

The position of the heart was as in *Trionyx*, but very little tilting was exhibited, the longitudinal axis of the heart being practically parallel to that of the body.

8. ***Amyda ferox spinifera (Trionyx spiniferus).*** (B.M. 59.9.20 : 26 ; from the United States.)

Weight of specimen = 248·3 g.
Dimensions of carapace = 14·5 × 12·1 cm.

The heart was similar to *Trionyx* as regards position and tilting.

9. ***Amyda ferox spinifera.*** Locality United States (presented by Dr. E. Malek, Tulane University Medical School, Lousiana). Two very young specimens.

Weight of one of the specimens = 8·3 g.
Dimensions of its carapace = 4·4 × 3·9 cm.

The heart of both specimens was definitely at the right side of the animal, its left border being just tangential to the mid-longitudinal axis, but no tilting whatsoever was exhibited.

10. ***Chitra indica.*** (B.M. 1921.4.1.197 from Ban Pong, C. Siam.)

The only alcohol-preserved specimen in the Museum and because of its large size it had to be cut into parts. It was not practicable to weigh or measure it. All the same the heart was in the same position as in *Trionyx*.

From the above data it may be deduced that the heart lies at the antero-right side of the body-cavity in all the known genera of the family Trionychidae. This fact, hitherto unrecorded, may be regarded as a general characteristic of the family.

The tilting of the heart seems to be a later development since in the new hatches (Nos. 7 and 9), the heart lies with its mid-longitudinal axis parallel to that of the body. This tilting may well be due to the pulling forces exhibited by the arterial arches on the left side of the body. These arteries extend from the heart in a roughly horizontal direction across the base of the neck to the left side of the body (Text-fig. 1, sub. art. l., car. art. l. and sys. art. l.). They run ventral to the huge central mass of muscles which causes retraction of the head and neck within the shell, namely the *retrachens capitis collique* of George & Shah (1955). The rapid growth of this muscle would cause some pressure on the arteries which, in their turn, would pull the antero-right part of the ventricle where they are attached. There is no counteracting pulling force from the right arterial arches since they do not run in the opposite direction, i.e. horizontally towards the right side, but extend anteriorly (Text-fig. 1, car. art. r. and sub. art. r.).

Except for the Trionychidae, all Chelonians have symmetrically situated hearts in the sagittal axis of the body. This is shown in drawings and descriptions by many early and recent writers, e.g. Bojanus (1819–21) in *Testudinia*; Martin & Moale (1805) in *Pseudemys*; Hoffmann (1890) in *Clemmys* and *Chelydra*; Burne (1905) and O'Donoghue (1918) in *Dermochelys*; Thomson (1932) in *Testudo* and Ashley (1955) in *Chelydra, Chrysemys* and *Pseudemys*. A sagittaly-situated heart was also found by the writer in *Chelys fimbriata* (B.M. 97.5.15.1; from Trinidad) and in *Pelomedusa galeata* (from Khartoum, Sudan).

Presence of an asymmetrically-situated heart in all genera of the family Trionychidae is very striking, and it is almost certain that it could not be incidental but a character that enables members of this family to live under certain conditions common to all of them.

In an effort to explain the relationship of the one-sided position of the heart and the life of these animals, two of their habits are noted:

(*a*) Soft-shelled turtles are expert swimmers as noticed by Agassiz (1857) who described their swimming movements; Garman (1892) who reported that the turtle can pursue and catch the quickest of fish and can swim against swift currents or dash away in danger, and Cahn (1937) who emphasized their swimming habits. A flat or low convex carapace gives them a great advantage as swimmers since it makes them more stream-lined and lessens water resistance.

(*b*) The flash-like way in which the head protracts to catch food, or retracts when the animal is frightened. As described by Boulenger (1889) "the neck is more perfectly adapted for complete and rapid retraction than in any other Chelonian".

Retraction of the head and neck in the Trionychids and in all the subclass CRYPTODIRA (where the neck withdraws in a sigmoid way) is effected by huge muscles situated in the sagittal axis of the body, the retrachens capitis collique.

Presence of the central mass of muscles in the CRYPTODIRA does not prevent these animals—the Trionychidae excepted—from having a perfectly symmetrical heart, but then they also have a highly convex or dome-shaped carapace to provide enough room to accommodate both. Such a carapace would certainly be a handicap to a good swimmer.

The shifting of the heart enables the Trionychids to have a shorter dorso-ventral axis and a more or less flat carapace which gives them a great advantage as swimmers, while still retaining the blessing of complete and flash-like retraction of the head.

It is quite possible that the shifting occurred as a result of the carapace and plastron having come nearer to each other. This possibility seems to be further confirmed by the fact that in *Cylanorbis*, where the dorso-ventral axis is deeper than in other members of the family owing to higher convexity of the carapace, the heart lies nearer to the mid-longitudinal axis of the body.

THE HEART OF *TRIONYX TRIUNGUIS*

To save unnecessary complications in describing the heart and blood vessels attached to it, the mid-longitudinal axis of the heart, *and not of the animal as a whole*, will be considered to indicate the antero-posterior direction ; and terms such as " medial " and " lateral " refer to the mid-axis of the heart and not of the animal.

(a) *Pericardium*

The pericardium is a rather thin, white serous membrane which surrounds the heart and the base of the arteries which extend from it. It is reflected to adhere to the outer surface of the collection of arteries, covering them completely within the pericardial cavity. The cavity is quite large, and it contains a faintly-yellowish watery fluid ; 11·5 c.c. of liquid were extracted from a medium-sized specimen (length of carapace 22 cm.).

The postero-dorsal wall of the pericardium is free and lies ventral to the anterior part of the right liver lobe. Here the surface of the liver is curved dorsally to make room for the heart. The antero-dorsal pericardial wall is firmly attached to the following parts (Text-figs. 2 and 3) :

(i) The sinus venosus which lies dorsal to the pericardium, outside the pericardial cavity (sin. v.).

(ii) The dorsal wall of the auricles, except for their short caudal ends which pass into the ventricles, and their anterior ends which are free.

(iii) The left anterior vena cava passes through the pericardium on its anterior left side and runs postero-medially around the edge of the left auricle (ant. v.c. l.). It penetrates the dorsal wall of the pericardium again and passes into the sinus venosus.

(iv) The right anterior vena cava (ant. v.c. r.) runs on the dorsal side of the pericardium, dorsal to the anterior border of the right auricle, and passes into the sinus.

(v) The left hepatic vein runs dorsal to the pericardium directly into the sinus (hep. v. l.). The terminal parts of the left anterior vena cava and left hepatic vein run on top of one another on opposite sides of the pericardium.

(vi) The proximal end of the posterior vena cava on its way to the sinus (post v.c.).

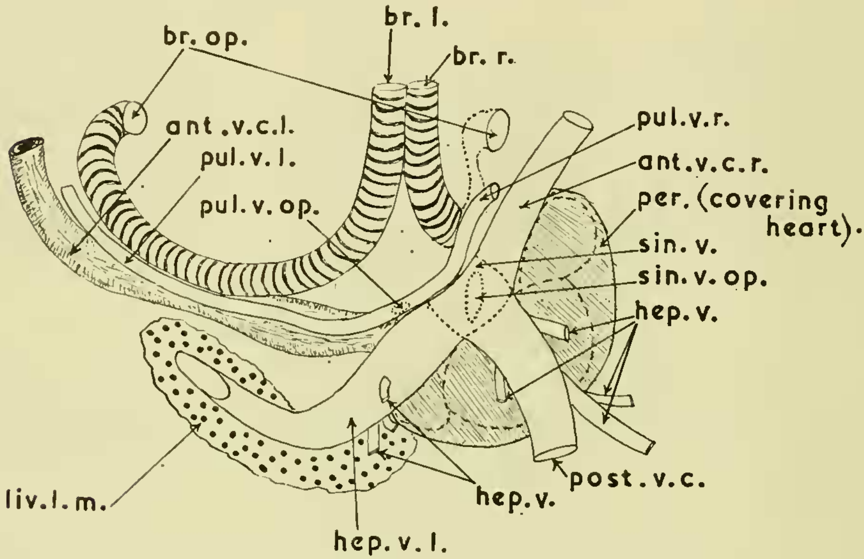

FIG. 2. *T. triunguis.* Dorsal dissection to show relative position of heart, veins and terminal bronchi. (Parts not seen are drawn in dotted lines.)

ant. v. c. l., left anterior vena cava ; ant. v. c. r., right anterior vena cava ; br. l., left bronchus ; br. op., bronchial opening into lung ; br. r., right bronchus ; hep. v., hepatic vein ; hep. v. l., left hepatic vein ; liv. l. m., medial liver lobe ; pei., pericardium ; post. v. c., posterior vena cava ; pul. v. l., left pulmonary vein ; pul. v. op., opening of pulmonary veins ; pul. v. r., right pulmonary vein ; sin. v., sinus venosus ; sin. v. op., opening of sinus venosus.

(vii) The pulmonary veins. The right pulmonary vein (pul. v. r.) runs horizontally anterior and adjacent to the right anterior vena cava, the sinus venosus, and the terminal parts of the left hepatic vein where it runs into its fellow of the other side (pul. v. l.). Their common opening into the left auricle may be seen by making a longitudinal incision in the walls of the vessels (pul. v. op.).

(viii) The coronary vein (Text-fig. 4, cr. v. dor.) runs from the antero-dorsal point at the right side of the medial axis of the ventricle, in a left and dorsal direction, and penetrates the pericardium to the sinus venosus. A shorter fibrous cord attaches the ventricle and the base of the coronary vein to the pericardium and may be termed ventriculo-pericardial ligament (Text-fig. 4, ven. per. lig.).

(b) *Chambers of the Heart*

1. *Sinus Venosus* (Text-figs. 2 and 3, sin. v.)

A dorsal dissection of the heart should be done by severing the heart and associated parts from the body, or alternatively by removal of the carapace and lungs.

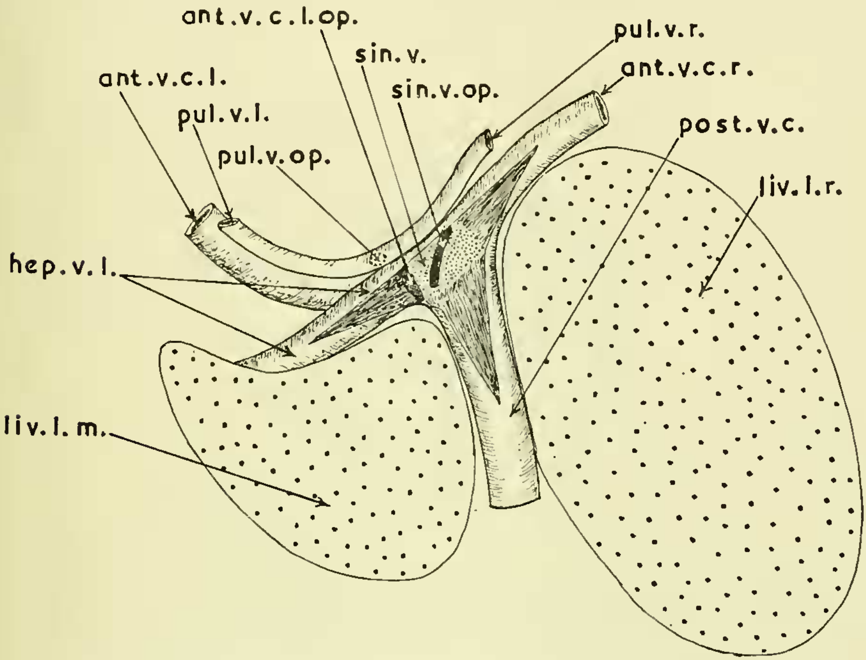

FIG. 3. *T. triunguis.* Dorsal wall of sinus venosus and veins removed to show the borders of the sinus and the oblique sinu-auricular opening. The openings of the left anterior vena cava (ventral) and of the left hepatic vein (dorsal) lie on top of one another.

ant. v. c. l., left anterior vena cava ; ant. v. c. l. op., opening of left anterior vena cava ; ant. v. c. r., right anterior vena cava ; hep. v. l., left hepatic vein ; liv. l. m., medial liver lobe ; liv. l. r., right liver lobe ; post. v. c., posterior vena cava ; pul v. l., left pulmonary vein ; pul. v. op., opening of pulmonary veins ; pul. v. r., right pulmonary vein ; sin. v., sinus venosus ; sin. v. op., opening of sinus venosus.

The sinus lies on the dorsal side of the pericardial wall on top of the medial part of the auricles, slightly nearer to the right side.

It can be seen dorsally as the part where the *left hepatic* vein, the *posterior vena cava* and the *right anterior vena cava* meet, but its actual borders may only be determined by making longitudinal incisions in the terminal parts of these veins (Text-fig. 3). A shallow ridge marks the border between the *posterior vena cava* and the sinus.

The *left hepatic* and the *left precaval* veins terminate on top of one another on the left side of the sinus, the formal being dorsal and the latter ventral (Text-fig. 3). The *right anterior vena cava* opens in the right aspect of the sinus, and the border is marked by a slight depression of the floor of the sinus which lies more ventrally. The anterior border of the sinus is adjacent to the terminal part of the *right pulmonary* vein.

The middle part of the floor contains the sinu-auricular opening which is spindle-shaped (oval in some specimens) and its long axis runs obliquely (Text-fig. 3, sin. v. op.).

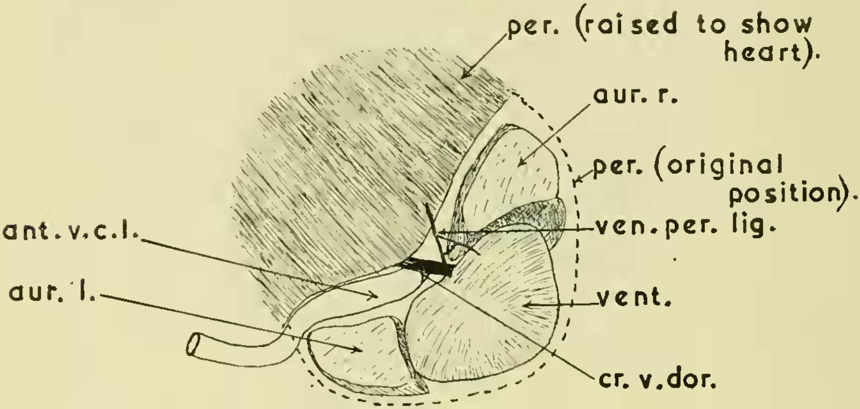

FIG. 4. *T. triunguis.* Dorsal aspect of heart. (Auricles are expanded and ventricle contracted.)

ant. v. c. l., left anterior vena cava ; aur. l., left auricle ; aur. r., right auricle ; cr. v. dor., dorsal coronary vein ; per., pericardium ; vent., ventricle ; ven. per. lig., ventriculo-pericardial ligament.

2. *Left Auricle*

The left auricle (Text-fig. 4, aur. l.) occupies roughly one-third of the anterior border of the two auricles and extends posteriorly for some distance dorsal to the ventricle. Its wall is comparatively thin. The common pulmonary opening (Text-fig. 2, pul. v. op.) is in the dorso-medial wall which is firmly attached to the pericardium and is very near the inter-auricular septum. It is an oval depression not guarded by valves.

The left auricular cavity extends as a narrow passage between the auricular wall externally, and the inter-auricular septum (Text-fig. 11, int. aur. sep.) internally. It ends in the left auriculo-ventricular opening at the left side of the dorsal base of the ventricle. The inner side of its wall and particularly on its dorsal aspect has a number of well-marked muscle strands, the " musculi pectinate " of O'Donoghue (1918).

3. *Right Auricle*

The cavity of the right auricle is the larger of the two. Not only is its anterior border about twice as long as that of the left auricle (Text-figs. 4 and 11), but also the wide passage which connects the auricles to the ventricle is almost completely a part of the right auricular cavity.

The walls are thicker than those of the left auricle especially at the right side where they show some depressions and bulgings comparable to some extent to those of the ventricular wall.

The sinu-auricular aperture lies in a dorso-medial position to the right side of the inter-auricular septum. It is guarded by a valve composed of two membranous semicircular flaps of tissue which overlap one another when closed.

The right auriculo-ventricular opening lies adjacent to the left one, the two openings being separated only by the thickness of the inter-auricular septum (Text-fig. 11, int. aur. sep.). Although nearer to the medial axis of the heart, the right opening is still on its left side. Mathur (1946) states that the left auricle opens into the left part of the cavum dorsale and the right opens into the right. This is not the case in *Trionyx triunguis* (and *Cyclanorbis oligotylus*).

4. *Ventricle*

Examining the heart from the ventral aspect (Text-fig. 8), the ventricle appears as a flat body with a bluntly rounded apex. The horizontal axis in the dilated condition is two and a half times as long as the antero-posterior axis. The right side is rather shorter than the left and they both taper towards the concave anterior base where the arterial arches originate. The roots of the arches occupy approximately the right two-thirds of the base.

Dorsally, the ventricle may be roughly described as deeply convex, with a larger posterior portion which ends in the round apex, and a smaller anterior one which slopes antero-ventrally to join the two sides of the ventricle.

No ligamentous attachment, " gubernaculum cordis ", as described by Ashley (1955) in painted turtles, by Mathur (1946) in *Lissemys punctata* and by O'Donoghue (1918) in *Dermochelys coriacea,* exists between the apex of the heart and the pericardium. During contraction of the heart, the ventricle shortens considerably towards its anterior base, and any ligamentous attachment of its apex to the pericardium, unless sufficiently long, would hinder its movements. The ventriculo-pericardial attachments here, are one or more short fibrous ligaments which extend from the antero-dorsal aspect of the ventricle to the dorsal wall of the pericardium (Text-fig. 4, ven. per. lig.), and the fibrous outer sheath of the coronary vein (Text-fig. 10B, ligament).

Internal Structure of the Ventricle

The internal structure and the ventricular cavity may be studied by cutting the organ transversely through the round apex and side wall, and opening it (Text-fig. 5), and also by making a number of dorso-ventral sections from apex to near base

(Text-fig. 6, Nos. 1–10). The terminal section which shows the auriculo-ventricular openings and their valves, and the three openings of the arterial arches (Text-fig. 7) is worthy of some special attention.

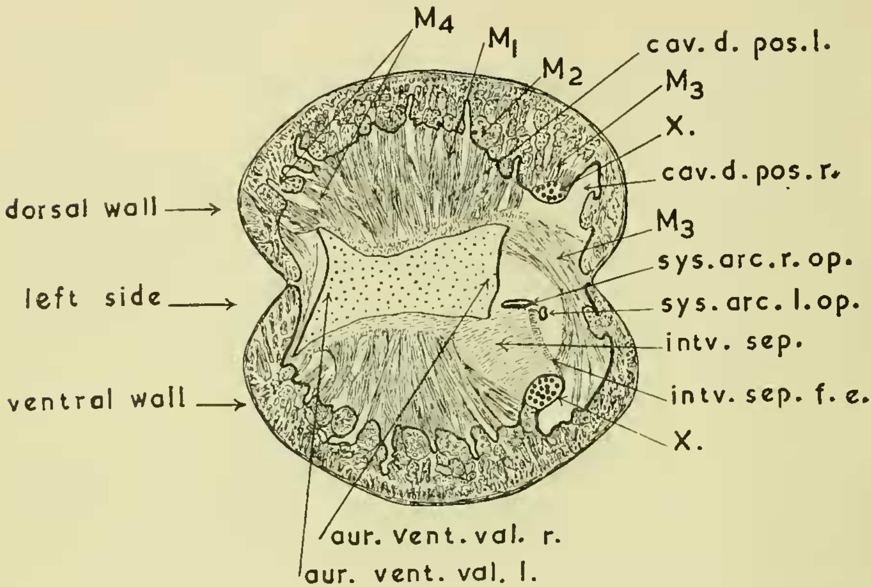

FIG. 5. *T. triunguis.* The ventricle opened horizontally from apex and sides. Internal view. The posterior part of the cavum magnum (c. dorsale) is divided by a short secondary septum into right and left parts. The cavum parvum (c. pulmonale) lies ventral to the inter-ventricular septum and is not in view.

aur. vent. val. l., left auriculo-ventricular valve; aur. vent. val. r., right auriculo-ventricular valve; cav. d. pos. l., posterior part of cavum dorsale, left cavity; cav. d. pos. r., posterior part of cavum dorsale, right cavity; intv. sep., inter-ventricular septum; intv. sep. f. e., free edge of inter-ventricular septum; M1, antero-posterior muscle fibres; M2, continuation of antero-posterior muscle fibres around apex; M3, right posterior to antero-medial muscle fibres; M4, left posterior to antero-medial fibres; sys. arc. l. op., opening of left systemic arch; sys. arc. r. op., opening of right systemic arch; x, secondary inter-ventricular septum.

(a) *Walls of the Ventricle* (Text-figs. 5, 6 and 7)

The wall is quite thick especially at the apex. The muscular tissue which forms the main thickness is composed of a network of bands of cardiac muscle fibres similar in structure to mammalian fibres. In the interstices of the muscle bundles there is a considerable amount of connective tissue. Numerous irregular cavities of variable sizes lie between the muscle bands so that the whole structure forms a rather loose spongy mass. Externally the wall is covered by a smooth serous membrane which, as in mammals, is composed mainly of connective tissue rich in elastic fibre. Internally the anterior part of the ventricular cavity is lined by a rather thick, white fibrous membrane which extends for some distance behind the auriculo-ventricular valves, and extends further to cover both surfaces of the inter-ventricular septum. The rest of the cavity is lined by a thin transparent continuation of the internal membrane.

Most of the muscle fibres are attached to dense fibrous membranes which lie round (i) the auriculo-ventricular openings, and (ii) the edge of the white membranous septum which lines the anterior part of the cavity. An account of the larger bands of muscle fibres follows :

(i) *Muscles of the Left Side* (Text-fig. 5, M.4)

The deeper bands are roughly " U "-shaped. They take origin from the left part of the anterior fibrous lining and run in a postero-left direction, with one limb in the dorsal wall and the other in the ventral wall, the two limbs running into each other around the left side of the apex. The bands nearer to the surface behave in a similar way, but their ends are attached to the fibrous skeleton of the heart around the left auriculo-ventricular junction. The main bands give branches which may either join other bands or are inserted into the outer coat, so that they are firmly attached to each other and to the outer coat.

(ii) *Muscles of the Middle Part*

The muscle bands in the middle part (Text-fig. 5, M1 and M2) behave likewise, but their direction is mainly antero-posterior.

(iii) *Muscles of the Right Part* (Text-fig. 5, M.3 and x)

The muscle bands which form the inter-ventricular septum (Text-fig. 5, intv. sep.) take origin from the right dorsal corner of the apex and run in an antero-medial and slightly ventral direction. They spread fan-wise as they proceed forward to terminate in the fibrous anterior wall. Some bands run dorso-ventrally into, or slightly to the left side of, the caudal end of the inter-ventricular septum (Text-fig. 5x) forming a short secondary septum which extends vertically between the dorsal, ventral and posterior walls and partly divides the posterior part of the ventricular cavity into a larger left and a smaller right portion (Text-fig. 6, Nos. 6 and 7).

The bands of the muscle fibres which form the floor of the right side of the ventricular cavity extend around the right wall of the ventricle and proceed anteriorly (Text-fig. 5, M.3). These are joined by other bands from the right wall, and the large resulting band runs medially and is inserted into the fibrous tissue (skeleton of heart), outside the right auriculo-ventricular junction.

(b) *The Auriculo-ventricular Openings and Valves*

The two openings (Text-fig. 7) lie side by side on the left dorsal base of the ventricle separated by a short septum, an extension of the inter-auricular septum (Text-fig. 11, int. aur. sep.). A transverse flap of fibrous tissue extends on either side of

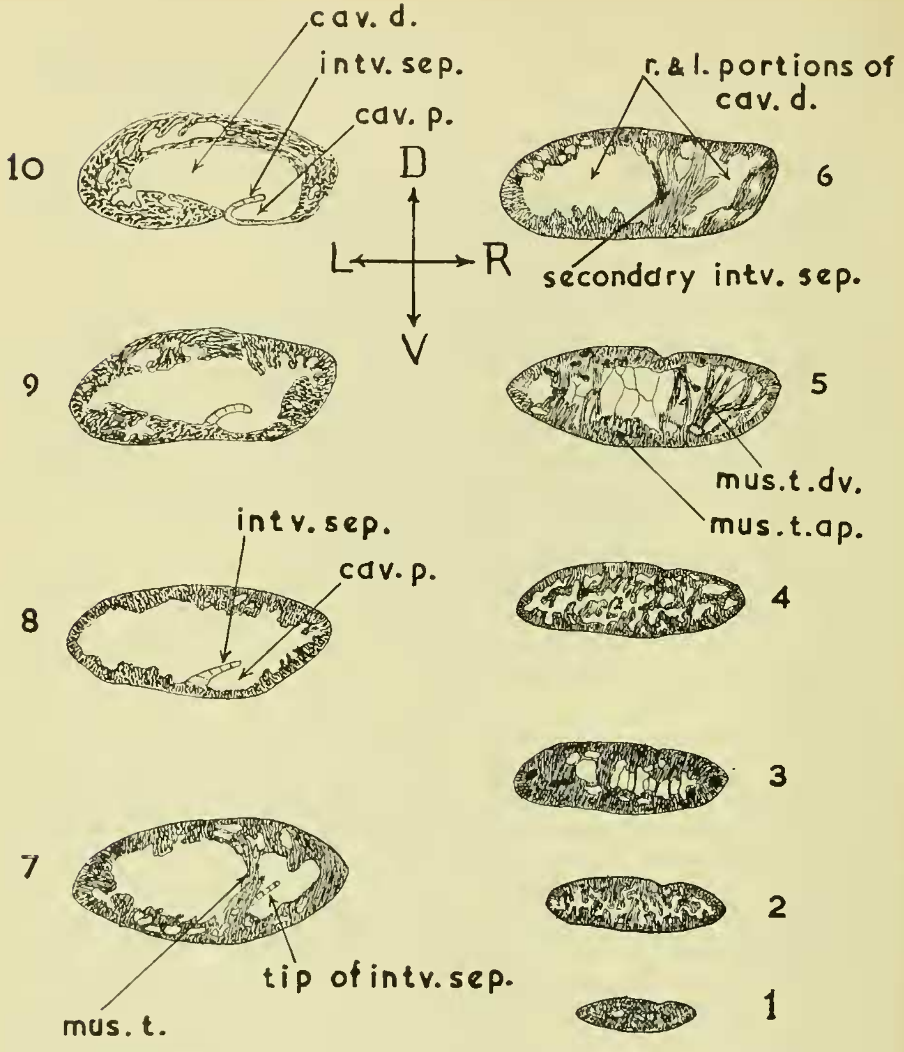

FIG. 6. *T. triunguis.* A series of dorso-ventral sections in the ventricle, parallel to the transverse axis. (Apex to near the anterior border.)

1–4. Spongy wall, with small irregular cavities. Muscle trabeculae run mainly antero-posteriorly and dorso-ventrally.

5. Muscle trabeculae are less in number and the cavities are larger.

6–7. Bands of muscle fibres cross the ventricular cavity in a dorso-ventral direction. They form a secondary inter-ventricular septum which divides the cavity into a larger left and a smaller right portion. The free edge of the inter-ventricular septum appears at the right side of the secondary septum.

8–10. Anterior ventricular cavity divided by the inter-ventricular septum into cavum dorsale (preferably magnum) and cavum pulmonale (preferably parvum).

cav. d., cavum dorsale ; cav. p., cavum pulmonale ; int. sep., inter-ventricular septum ; mus. t., muscle trabecule ; mus. t. ap., antero-posterior muscle trabecule ; mus. t. dv., dorso-ventral muscle trabecules.

the septum to form the two auriculo-ventricular valves (Text-figs. 5 and 7, aur. vent val.). The valves are attached to the dorsal and ventral walls of the ventricle cutting off an anterior passage from the ventricular cavity. The left valve is comparatively short and its funnel-like opening is adjacent to the left ventricular wall. The right valve is longer and its opening lies at some distance from the right wall of the ventricle.

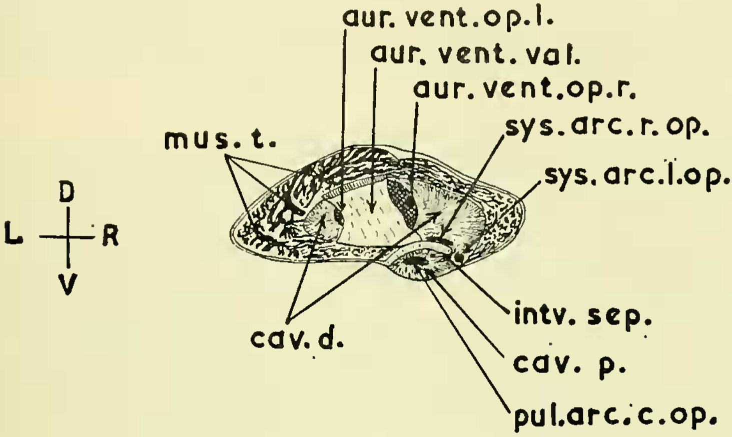

FIG. 7. *T. triunguis.* Anterior part of ventricle cut dorso-ventrally parallel to the transverse axis. Posterior view to show internal structure.

aur. vent. op. l., left auriculo-ventricular opening ; aur. vent. op. r., right auriculo-ventricular opening ; aur. vent. val., auriculo-ventricular valve ; cav. d., cavum dorsale ; cav. p., cavum pulmonale ; intv. sep., inter-ventricular septum ; mus. t., muscle trabecule ; pul. arc. c. op., opening of common pulmonary arch ; sys. arc. l. op., opening of left systemic arch ; sys. arc. r. op., opening of right systemic arch.

(c) *Cavities of the Ventricle*

The ventricle contains mainly two cavities connected with each other (Text-fig. 6, No. 10 and Text-fig. 7). The larger cavity is dorsal and extends from one side of the ventricle to the other, and is termed the " cavum dorsale " (cav. d.). The smaller cavity occupies the ventral and right position, and has been called the " cavum pulmonale " or " cavum ventrale " (cav. p.). The terms are common and have been used by most authors, e.g. O'Donoghue (1918), Goodrich (1919), Mathur (1946), Thomson (1932), Foxon (1955) and others. It is suggested, however, that the terms " cavum magnum " and " cavum parvum " would give a more accurate naming for the cavities which are not strictly dorsal and ventral to each other.

The two cavities are separated by an inter-ventricular septum (intv. sep.) which takes origin from the ventral wall, its line of attachment being roughly from a postero-medial point to an antero-right one (Text-fig. 11, intv. sep. b.). The septum extends towards the right side, sloping slightly dorsally to end in a free edge (Text-fig. 5, intv. sep. f.e.) near, and to some extent parallel to the right wall of the ventricle. The white membranous lining of the ventricular cavity extends on both surfaces of the septum.

Towards the posterior end, the cavum magnum (dorsale) is partially divided into right and left cavities by a secondary septum (Text-fig. 6, Nos. 6 and 7, and Text-fig. 11, x) which, however, is very short and is not effective in dividing the dorsal ventricular cavity.

More posteriorly (Text-fig. 6, No. 5—1) the muscle bands and trabecules increase more and more in number breaking the ventricle into intercommunicating small cavities. Finally we come to the thick outer serous membrane.

(d) *Internal Openings of the Arterial Arches* (Text-fig. 7)

The three arches open near one another at the antero-right side of the ventricle. The pulmonary opening is the largest, the left systemic the smallest, and the right systemic intermediate.

The pulmonary opening (pul. arc. c. op.) lies at the anterior end of the cavum parvum (pulmonale) in the ventral wall of the ventricle near its base. The left systemic opening (sys. arc. l. op.) also lies at the ventral wall, at the right side of the free edge of the inter-ventricular septum. It is quite near the right wall of the ventricle. The opening may be described as situated just outside the entrance of the cavum parvum (pulmonale). The right systemic opens at the base of the dorsal wall of the ventricle, close but somewhat to the left side of the left systemic (sys. arc. r. op.). The two systemics do not open immediately behind the auriculo-ventricular apertures as in the species described by Mathur (1946).

Each of the openings of the arterial arches is guarded by two semi-lunar valves similar in structure to those of mammals. They proved to be equally efficient as it was not possible to inject the ventricle through any of these arches.

(c) *Arterial Arches* (Text-figs. 8 and 9)

The *common pulmonary arch* (pul. arc. c.) to the left, and the *left systemic arch* (sys. arc. l.) to the right, run from the base of the ventricle in an antero-left direction. The *right systemic arch* lies dorsal to them and cannot be seen in a ventral view, but its main branch, the *innominate* artery (innom. art.) is partly visible. A semi-transparent membranous sheath reflected from the pericardium envelopes all the arteries, and several ligamentous processes connect their walls together. Very careful dissection is necessary to separate the arteries without injury and excessive bleeding. It is advisable to inject the circulatory system with formalin and leave the animal for some time in formalin before attempting to dissect the heart and blood vessels attached to it. The vessels would then be dilated and better demonstrated.

The *common pulmonary arch* proceeds forwards for a short distance and then bifurcates into the *right* and *left pulmonary arches*. The former (Text-fig. 9, No. 2, pul. arc. r.) takes a sharp curve to the right side, practically at right angles to the *common pulmonary arch*, and dorsal to the collection of arteries, so that it is not in view in a ventral dissection. It leaves the pericardial cavity opposite the antero-ventral border of the right auricle.

The *left pulmonary arch* (pul. arc. l.), the *left systemic arch* (sys. arc. l.), the *left subclavian* (sub. arc. l.) and the *left carotid* arteries (car. art. l.)—the carotid and subclavian having just emerged from the innominate—take a straight antero-left course and pass through the pericardium (Text-fig. 9, Nos. 2 and 3). Before penetrating

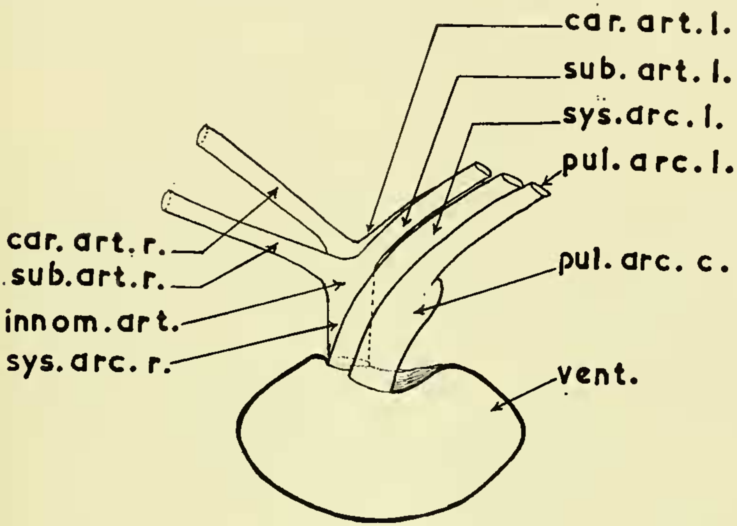

Fig. 8. *T. triunguis.* Arterial arches and their branches as seen in a ventral view.

car. art. l., left carotid artery ; car. art. r., right carotid artery ; innom. art., innominate artery ; pul. arc. c., common pulmonary arch ; pul. arc. l., left pulmonary arch ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sus. arc. l., left systemic arch ; sys. arc. r., right systemic arch ; vent., ventricle.

the pericardium, the *left carotid* is hidden from view in the ventral dissection, as it lies dorsal to the *left subclavian* (Text-fig. 8).

The *right systemic arch* shortly after its origin from the ventricle, gives off the *innominate* artery which is as wide as the arch itself, so that it is difficult to distinguish at a glance which is the origin and which is the branch (Text-fig. 9, Nos. 2 and 3). A longitudinal dorsal incision gives the answer as it shows the inner orifice of the *innominate* in the ventral wall of the *right systemic.* As soon as it gives off its great *innominate* branch, the *right systemic* bends sharply to the right, forming a loop (Text-fig. 9—2) and penetrates the pericardium very near to the exit of the *right pulmonary arch.* The *innominate* artery starts branching while still in the pericardial cavity. A longitudinal dorsal incision (Text-fig. 9—4) helps considerably in following its branches which are extremely close to each other and quite confusing. After a short straight course, the dorsal wall of the *innominate* artery terminates by bifurcating into a wider *right carotid* artery and a narrow *left carotid* artery. The *right subclavian* starts from an orifice (Text-fig. 9, No. 4, sub. art. r. op.) in the ventral wall of the innominate at a short but quite distinguishable distance behind the *right carotid*. The *left subclavian* artery likewise originates from the ventral wall of the *innominate* but its orifice (sub. art. l. op.) is almost ventral to that of the

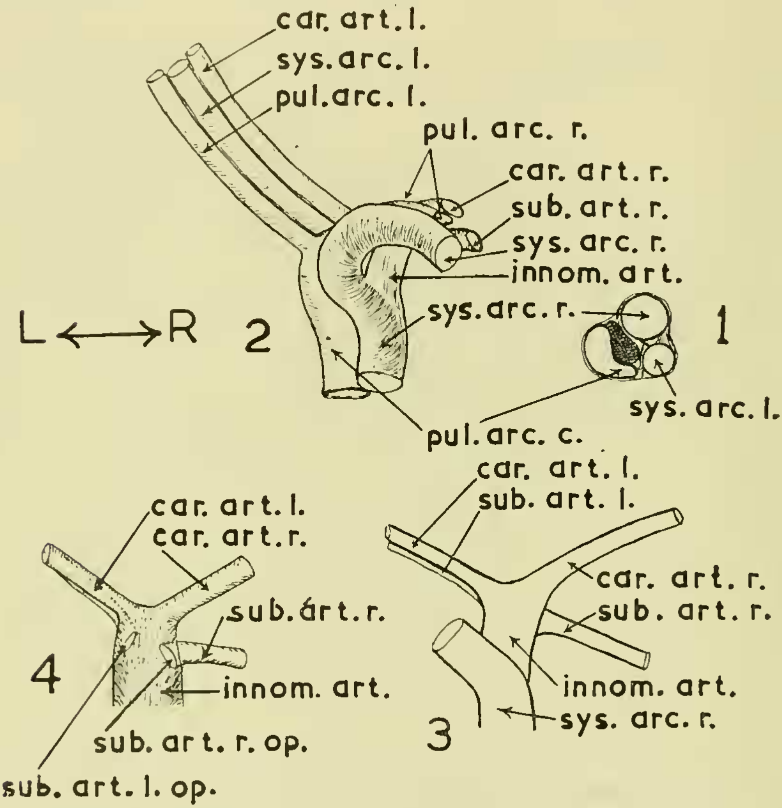

FIG. 9. *T. triunguis.* Arterial arches and their branches from the dorsal aspect.

1. T.S. at exit of arches from ventricle.
2. Arterial arches and their branches.
3. Innominate artery; its four branches seen after removal of part of the right systemic arch (which loops to the right side and covers them).
4. Innominate artery opened by a longitudinal incision to show exit of its four branches.

car. art. l., left carotid artery; car. art. r., right carotid artery; innom. art., innominate artery; pul. arc. c., common pulmonary arch; pul. arc. l., left pulmonary arch; pul. arc. r., right pulmonary arch; sub. art. l. op., opening of left subclavian artery; sub. art. r. op., opening of right subclavian artery; sys. art. l., left systemic arch; sys. arc. r., right systemic arch.

left carotid so that the two arteries run on top of each other until shortly after passing through the pericardium. The *right carotid* and *right subclavian* arteries proceed through the antero-right pericardial wall, the *right carotid* being medial and the *right subclavian* lateral to each other.

The *carotid* is usually described as a branch of the *subclavian* artery of the corresponding side, or both arteries as branches of a *branchiocephalic* artery. Ashley (1955) considers the *branchiocephalic* artery (innominate) as bifurcating to form two large branches each of which gives off two branches in close succession. In *T. triunguis*, however, the four arteries are quite separate and each has its own origin from the *innominate* artery.

(d) *Coronary Circulation* (Text-fig. 10, A and B)

1. *Arteries*

The *coronary* artery (cr. art.) may originate from the base of the *right subclavian* artery (sub. art. r.), or from the adjacent *innominate* artery. It runs in the fibrous sheath which surrounds the arterial arches, along their right side to the anterior border of the ventricle. The artery then bifurcates into a *ventral coronary* (cr. art. vent. b.) and a *dorsal coronary* artery (cr. art. dor. b.). The *ventral coronary* artery runs along the ventral side of the anterior border of the ventricle, and gives smaller branches which run down the ventral wall towards the apex. The *dorsal coronary* artery runs along the dorsal side of the anterior ventricular border and gives some branches to the dorsal wall of the ventricle, as well as right and left *auricular* branches to the posterior walls of the right and left auricles respectively (aur. l. cr. art.).

2. *Veins*

(*a*) Veins from the ventral wall of the ventricle run into a *ventral coronary vein* (cr. v. vent.) which runs at the ventral side of the anterior border of the ventricle adjacent to the corresponding coronary artery, and proceeds along the side of the main coronary artery to terminate in the *right anterior vena cava*.

(*b*) Three veins collect the blood from the right, the middle and the left parts of the dorsal wall of the ventricle. The left vein receives a *branch* from the posterior wall of the left auricle (aur. l. cr. v.) and the right from the right auricle. The three veins join together to form the *dorsal coronary veins* (cr. v. dor.) which passes through the pericardium and terminates in the *sinus venosus*. The dorsal coronary vein is protected by a strong fibrous sheath which also helps to fix the antero-dorsal border of the ventricle to the pericardium (Text-fig. 10, ligament).

(e) *Heart Beat*

In specimens freshly killed by chloroform, the heart continues to beat for a considerable length of time after the apparent death of the animal. Hearts removed from the body and placed in saline solution behaved in a similar manner. Johnson, Clinton & Stevens (1957) report a turtle heart beating 5 days after death.

The number of heart beats in several anaesthetized specimens (weight 4–26·5 kg.), varied between 16 and 29 per minute in different individuals.

The dorsal position of the sinus makes it very difficult to observe in the living animal. It may be reached by inserting a finger gently above the ventricle, but contractions of the sinus could not be felt by finger touch. Yet when the heart, together with the attached blood vessels and adjacent part of liver, had been removed from the animal and put in saline, the rhythmic contractions of the sinus were seen. The contractions were quite feeble, compared to the other chambers of the heart.

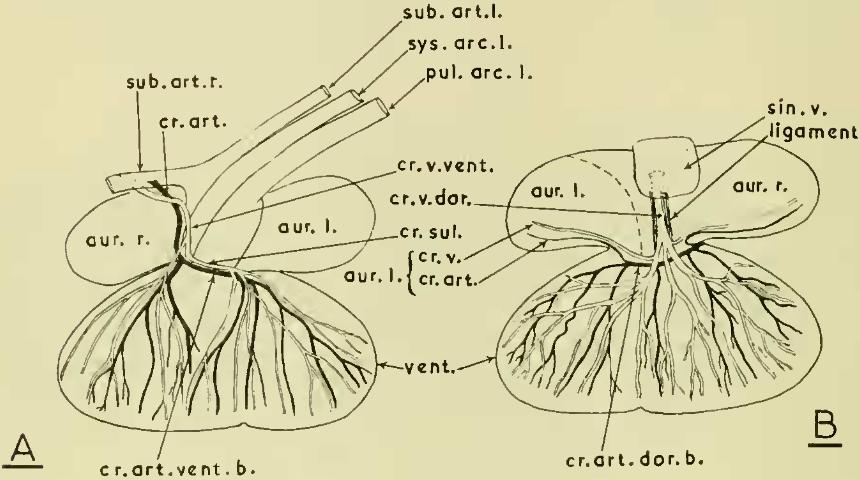

FIG. 10. *Cyclanorbis oligotylis*. Coronary circulation.

A. Ventral view.

B. Dorsal view.

aur. l., left auricle ; aur. r., right auricle ; aur. l cr. art., left auricular coronary artery ; aur. l. cr. v., left auricular coronary vein ; cr. art., coronary artery ; cr. art. dor. b., dorsal branch of coronary artery ; cr. art. vent. b., ventral branch of coronary artery ; cr. sul., coronary sulcus ; cr. v. dor., dorsal coronary vein ; cr. v. vent., ventral coronary vein ; pul. arc. l., left pulmonary arch ; sin. v., sinus venosus ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sys. arc. l., left systemic arch ; vent., ventricle.

The two auricles beat simultaneously, and the ventricle follows immediately. Watching the movement from a ventral view, the auricles were seen to contract strongly at their antero-medial tip. Their middle and postero-lateral parts followed in quick succession, and simultaneously the dorso-ventral diameter shortened considerably, bringing the ventral wall nearer to the dorsal one. The ventricle contracted in a peculiar way. Its left side started the movements by an abrupt shortening of both longitudinal and vertical diameters, bringing the left part of the round apex forwards and slightly medial. The wave of contraction passed towards the right side which terminated the movements by a noticeably strong contraction. The ventricle remained in the contracted condition for a short while, its right side being slightly shorter than the left, and its deep red colour fading to a much paler shade. Beats succeeded one another regularly, a short pause following each ventricular systole.

While most workers agree that the rhythmic contraction of the heart is a specific immanent property of the cardiac muscle itself, there is some difference as to whether the muscle connecting the cardiac chambers has special histological characters which differentiate it from the general myocardium. Davies & Francis (1945) made a comprehensive review on heart contraction in poikilothermal and homiothermal vertebrates and showed that so far as the anatomical studies are concerned the more recent workers are in a reasonable agreement that there is no histological specialization of any part of the cardiac musculature in poikilothermal animals.

As regards the route of the contraction wave, the following work in the Chelonian heart is of special importance. Meek & Eyster (1912) used electrocardiographic methods and found that the wave passes over the heart from the sinus, right auricle, left auricle, base of the ventricle and apex of ventricle. Lowman & Laurens (1924) found that the right and left parts of the auriculo-ventricular funnel are more efficient than the dorsal and ventral for conducting the impulse to the ventricle. Ishihama (1927), by cutting parts of the auriculo-ventricular junction observed that the right and left lateral parts conduct the impulse most readily, the ventral part less easily, and the dorsal part and the atrial septum not at all. Lewis (1916), and Holzlöhner (1930) determined electrocardiographically in fish, amphibia and reptiles that the middle level of the ventricle is the first part to receive the stimulus from the atria, and that the wave of contraction proceeds thence towards the apex and base. Scholomovitz & Chase (1916) observed the effects of the localized warming, cooling, or electric stimulation and showed that the primary pacemaker is a definitely localized portion of the sinus wall, on the right side of the sinus-auricular junction.

(f) *Double Circulation in the Heart* (Text-fig. 11)

Oxygenated blood pours continuously into the left auricle and deoxygenated blood into the sinus venosus. The openings of the veins into these parts are not guarded by valves, contraction of the sinus drives the blood into the right auricle.

The sinu-auricular opening is guarded by a valve made of two flaps of tissue which, when the auricle becomes full, overlap and close the opening.

Contraction of the auricles drives the blood into an empty ventricle. The *auriculo-ventricular valves* play an important part in directing the course of the blood. Oxygenated blood passes through a short passage between the anterior border of the ventricle and the flap of tissue which forms the left part of the valve, and is directed to the extreme left aspect of the ventricle. The right side passage is longer but it does not take the blood all the way to the right end as its stops about half-way through the transverse diameter of the-ventricle. Nevertheless, its opening points to the right, and blood coming in jerks under pressure of contractions of the right auricle is pushed into the right side of the ventricle, dorsal to the inter-ventricular septum and around its free edge, into its goal, the cavum parvum (pulmonale) It was pointed out that the wall of the right auricle contained strong muscle fibres comparable with those of the ventricle. These muscles should provide the necessary force required to push the blood all the way through.

The cavum parvum (pulmonale) will thus be filled with nothing but deoxygenated blood. Its small volume as compared with that of the right auricle suggests that it cannot possibly accommodate all the deoxygenated blood received at each auricular

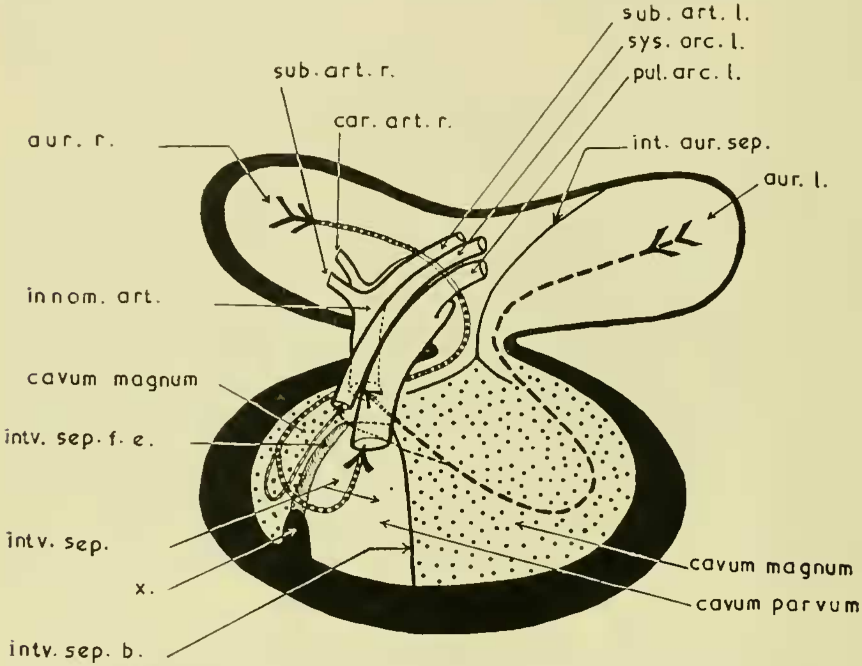

FIG. 11. *T. triunguis.* Diagram of heart and circulation, ventral aspect. Part of the cavum magnum lies under (dorsal to) the cavum parvum.

aur. l., left auricle ; aur. r., right auricle ; car. art. r., right carotid artery ; innom. art., innominate artery ; int. aur.sep., inter-auricular septum ; intv. sep., inter-ventricular septum ; intv. sep. b., base of inter-ventricular septum ; intv. sep. f. e., free edge of inter-ventricular septum ; pul. arc. l., left pulmonary arch ; sub. art. l., left subclavian artery ; sub. art. r., right subclavian artery ; sys. arc. l., left systemic arch ; x., secondary inter-ventricular septum.

systole. Therefore, some deoxygenated blood remains in the right side of the ventricle both in the ventral part outside the entrance of the cavum parvum (pulmonale) and in the dorsal part which is continuous with the cavum magnum (dorsale).

Oxygenated blood is now at the left part of the cavum magnum and a considerable proportion of it finds its way to the numerous little cavities in the spongy wall of the ventricle. Mixing of the blood in the middle part of the cavum magnum is unavoidable.

The ventricle having been filled with blood, starts to contract :

1. The left part of the ventricle contracts first, driving its blood towards the right side. Consequently, blood in the right side is forced out of the ventricle into the arterial arches.

(*a*) Deoxygenated blood in the cavum parvum passes into the pulmonary arch, and is replaced by deoxygenated blood from just outside the cavum parvum.

(*b*) Deoxygenated and mixed blood pass into the left systemic arch.

(*c*) Maybe some mixed blood from the middle part, and for the most part oxygenated blood from the left part of the cavum dorsale, pass into the right systemic arch.

2. The right side of the ventricle contracts strongly, while the left side remains in the contracted position until the blood is expelled. Judging by the colour of the ventricle in this condition, very little, if any blood remains trapped in the spongy cavities of its wall.

(*a*) Deoxygenated blood in the cavum parvum passes out through the pulmonary arch. The wall of the ventricle comes in contact with the edge of the inter-ventricular septum cutting off the cavum parvum from the rest of the ventricle.

(*b*) Mixed and maybe some oxygenated blood pass through the left systemic.

(*c*) Oxygenated blood passes through the right systemic. The oxygenated blood in the cavities of the left side of the spongy wall has little chance to mix with deoxygenated blood and is the last blood to leave the ventricle.

To summarize :

The pulmonary arch receives deoxygenated blood, the left systemic receives mixed blood ; and the right systemic receives some mixed and for the main part, oxygenated blood.

THE HEART OF *CYCLANORBIS OLIGOTYLUS*

The heart is similar in its main features to the heart of *T. triunguis* but the following differences were noticed :

1. *Position of the Heart*

The heart lies nearer to the sagittal axis of the body which passes through the left side of the left auricle.

2. *Pericardial Cavity*

The cavity is much larger in *Trionyx*. The carapace in *Cyclanorbis* is more convex and therefore the dorso-ventral axis at the site of the heart is deeper in *Cyclanorbis* and allows for a deeper cavity. In a medium-sized specimen (length of carapace 23 cm.) 25 c.c. of pericardial fluid were extracted from the cavity, while 11·5 c.c. only were obtained from a comparable specimen of *Trionyx*.

3. *External Appearance*

The apex of the ventricle is not bluntly rounded especially during systole, but has a flat appearance with an obvious notch which lies slightly to the right side of the medial axis (Text-fig. 12). The hearts of the two species are, therefore, quite easily differentiated from one another.

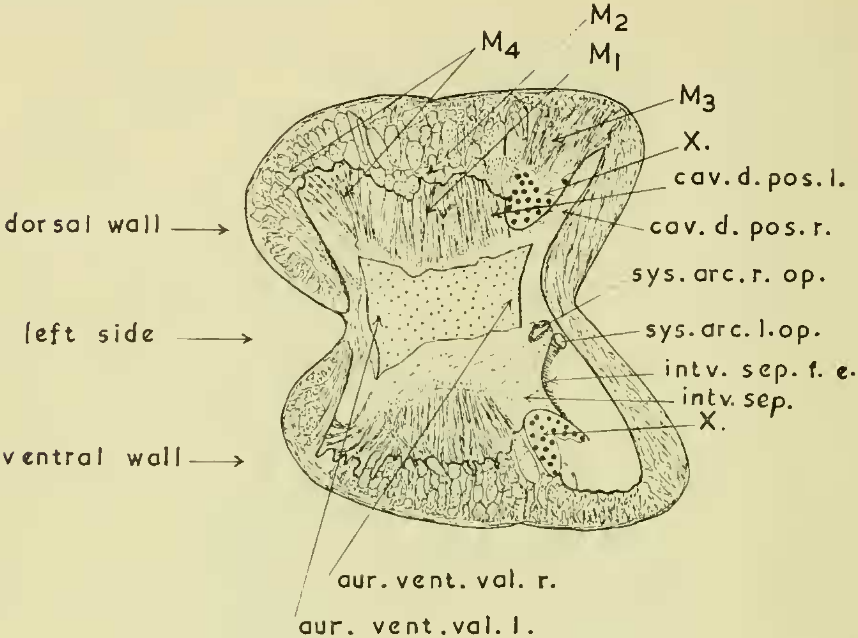

FIG. 12. *C. oligotylis.* Ventricle opened horizontally from apex and sides, internal view. The secondary inter-ventricular septum divides the posterior part of the cavum magnun (c. dorsale) into right and left cavities. The cavum parvum (c. pulmonale) lies ventral to the inter-ventricular septum and is not in view. Most of the antero-posterior muscle fibres are continuous around the apex where they are intermingled with some dorso-ventral muscle fibres and some white fibres inserted in the outer coat.

aur. vent. val. l., left auriculo-ventricular valve ; aur. vent. val. r., right auriculo-ventricular valve ; cav. d. pos. l., posterior part of cavum dorsale, left cavity ; cav. d. pos. r., posterior part of cavum dorsale, right cavity ; intv. sep., inter-ventricular septum ; intv. sep. f. e., free edge of inter-ventricular septum ; M1, antero-posterior muscle fibres ; M2, continuation of antero-posterior muscle fibres around apex ; M3, right posterior to antero-medial muscle fibres ; M4, left posterior to antero-medial fibres ; sys. arc. l. op., opening of left systemic arch ; sys. arc. r. op., opening of right systemic arch ; x, secondary inter-ventricular septum.

4. *Internal Structure* (Text-fig. 12)

A prominent muscular secondary septum (x) divides the posterior part of the cavum magnum (dorsale) into a larger left portion (cav. d. pos. l.), the *cavum sinistrum*, and a much smaller right one (cav. d. pos. r.), the *cavum dextrum.* The septum starts as a few bands of muscular and fibrous tissue which originate from the posterior wall near the dorsal right corner of the apex of the ventricle and run antero-medially and ventrally towards the posterior end of the free edge of the inter-ventricular septum. Here the fibres aggregate to form a fairly thick band which is further enlarged by additional bands which run in a dorso-ventral direction and join the main bulk at its left side. A secondary septum is thus formed which extends between the dorsal, ventral and posterior walls.

From the edge of the secondary septum the fibres spread fanwise as they proceed anteriorly in the ventral wall of the ventricle to terminate in the anterior border of its base. The spreading out of the fibres reduces their depth and leaves a clear anterior passage between the left and right sides of the ventricular cavity.

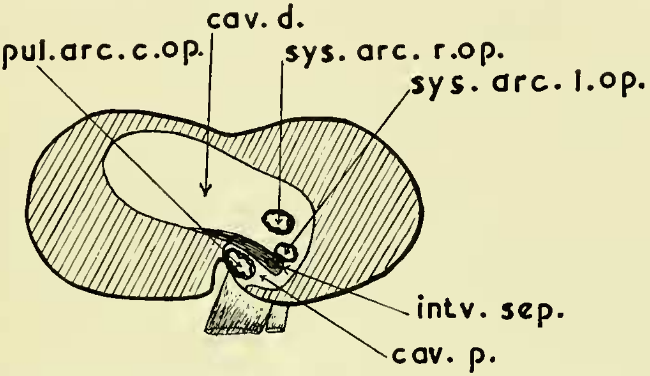

FIG. 13. *C. oligotylis.* Posterior view of a dorso-ventral section in the anterior part of the ventricle to show the openings of the arterial arches in the ventricular cavities.

cav. d., cavum dorsale; cav. p., cavum pulmonale; intv. sep., inter-ventricular septum; pul. arc. c. op., opening of common pulmonary arch; sys. arc. l. op., opening of left systemic arch; sys. arc. r. op., opening of right systemic arch.

The secondary septum in *T. triunguis* is less prominent and is nearer to the posterior wall, so that the division of the cavum magnum posteriorly into two cavities is not as sharp and clear as in *C. oligotylus.*

The position of the openings of the arterial arches (Text-fig. 13) shows no difference from *T. triunguis.*

5. *Heart Beat*

The two auricles contract in the same way as in *T. triunguis* driving the blood to the ventricle, which enlarges considerably. Ventricular systole follows; the left side of the ventricle contracts first and the right side immediately afterwards, the whole ventricle remaining in the contracted condition for an interval during which its wall changes colour from dark red to pale pink as blood drains out. Heart beats succeed one another in the same way. The number of beats varied between 19 and 21 per minute in five specimens but in each case the animal was injected with 5 c.c. of chloroform and opened after its apparent death. The counting, therefore, was not done under normal conditions.

The main difference from *T. triunguis* is the noticeable separate contraction of each of the two sides of the ventricle, while in *Trionyx* there is one long wave of contraction which starts at the left side and terminates at the extreme right.

6. *Circulation*

Separation of the oxygenated and deoxygenated blood seems to be more effective than in *T. triunguis*. In addition to the numerous little cavities in the muscular wall of the ventricle which accommodate a certain proportion of blood, a round opening near the left auriculo-ventricular opening leads to an irregular cavity within the ventral wall of the ventricle, and, judging by the position and size of this cavity it holds a fairly large quantity of oxygenated blood. Blood within the cavities in the wall has no chance to mix until it passes out into the main ventricular cavity on its way to the arterial arches.

The *secondary interventricular septum*, by dividing the posterior part of the cavum magnum into right and left cavities, is another factor in minimizing the mixing of the two types of blood. The deoxygenated blood pushed into the ventricular cavity passes to the right side of the secondary septum into the right cavity as well as around the free edge of the original septum into the cavum parvum (pulmonale). Blood in the right cavity has free access to the cavum parvum (pulmonale). However, as the secondary septum does not extend to the anterior border of the ventricle, some mixing of blood is bound to happen.

6. *Abnormalities*

Some individual differences were noticed in a number of specimens, for example :

(*a*) A thread-like fibrous ligament (gubernaculum cordis) extended between the dorsal side of the ventricle near its apex to the antero-dorsal part of the pericardium. Its length was over double the length of the heart.

(*b*) The dorsal coronary vein in a specimen had its three main branches running separately, only joining each other just before entry of the vein into the sinus venosus. These branches normally combine before the vein leaves the ventricle.

(*c*) The fibrous ligaments which join the antero-dorsal border of the ventricle to the pericardium vary in number and do not always follow the same pattern. Occasionally, ligaments have been found between the auricle and ventricle.

Oxygen Saturation in the Right and Left Systemic Arches, the Pulmonary Arch and the Two Auricles

Little experimental work has apparently been done on the circulation of reptiles. Prakash (1952) used radiological methods in the lizard *Uromastyx hardwickii* and stated that there is very considerable mixing of arterial and venous blood in the heart. Foxon & Price (1953) state (in a preliminary report) that radiographic experiments indicate, in *Lacerta viridis*, the existence of considerable separation of the arterial and venous streams of blood and that probably there is little difference in the type of blood conveyed by right and left systemic arches. Foxon (1955) states, in an addendum to the paper, that the results of using improved radiographic methods confirm the view that there is considerable separation of arterial and venous blood in the ventricle, but they also show a functional division of the cavum dorsale of the ventricle which results in the right systemic artery conveying more highly oxygenated blood than the left. Yet Steggerda & Essex (1957) in the turtle *Chelydra serpentina* having recorded oxygen saturation, blood-saturation dye curves and pressure measurements in the cardiac chambers and arteries leaving the heart, state that the *saturation levels of the blood leaving the heart via the right and left aortae are the same* while pulmonary artery blood is distinctly more venous.

The description of heart circulation in the previous chapter was based on anatomical features alone, but the conflicting results given by Steggerda & Essex necessitated the addition of a very short " experimental " part to investigate this point.

Method. Experimental animals were of the large size whenever possible as 25 ml. of blood were required to be drawn from each. The animal was subjected to mechanical insufflation at the rate of 15 times a minute. The amount of ventilation was adjusted so that with each cycle there was a noticeable raising and lowering of the ventral body wall and heart. This was allowed to continue for at least 20 minutes before samples of blood were taken.

A lightly oiled, 10 ml. syringe was used and its dead space was filled with oxalate solution made as follows : 4 g. potassium oxalate + 6 g. ammonium oxalate in 100 c.c. water. Heparine solution 1/1,000 as used for blood of mammals was tried but failed as blood was found to clot after some time. Blood was drawn from the three arteries, one at a time, and then from each auricle in the order shown below, but samples from the auricles were not taken when the heart did not contain enough blood to give a slow but steady supply to the syringe. Blood samples were collected in polythene bottles under oil.

Sample 1. The base of the left subclavian was pricked, and the needle driven into the innominate artery (see Text-fig. 9). The sample represents the right systemic.

Sample 2. From the base of the left systemic.

Sample 3. From the common pulmonary arch.

Sample 4. From the right auricle.

Sample 5. From the left auricle.

The samples were analysed in the Department of Physiology, Faculty of Medicine, University of Khartoum, by the electrophotometric method. Results were later reported to the writer, signed by the analyst of the Department (Dr. Nasr El Din)—see Table I.

Conclusion

(1) Oxygen saturation in the right systemic artery is higher than in the left, and in the left systemic artery higher than in the pulmonary.

(2) Oxygen saturation in the pulmonary arch is slightly higher than in the right auricle, which shows that a small quantity of oxygenated blood mixes with venous blood as it passes through the heart.

TABLE I.—*Oxygen Saturation in the Three Aortic Arches and the Two Auricles of* Trionyx triunguis

Experiment No.	Weight in kg.	Number of beats per minute	% oxygen saturation pulm.	l. sys.	r. sys.	r. aur.	l. aur.
1	5·14	16	55	80	95	50	95
2	5·08	16–17	60	85	97	50	97
3	2·19	16	55	78	90	45	—
4	7·55	17	52	70	85	50	86
5	8·65	22–0	—	—	—	—	—
6	26·66	28	55	60	90	50	95
7	5·57	20	33	55	80	—	—
8	11·10	20–21	55	78	85	53	85
9	4·14	29	30	45	70	—	—
10	14·32	22	50	70	82	—	—
11	17·95	23	55	60	85	45	85
Average saturation in 10 experiments			50	68·1	85·9	—	—
Average in 6 experiments where samples from both auricles were taken. Nos. 3, 7, 9 and 10 exlcuded			55·3	72·1	89·5	49·7	90·5

(3) Oxygen saturation in the left auricle is very slightly higher than in the right systemic, which shows that practically all oxygenated blood passes into the right systemic.

These results agree with anatomical findings. The statement of Steggerda & Essex (1957) that saturation levels of the blood leaving the heart via the right and left aortas are the same could *not* be true for *Trionyx*.

DISCUSSION

1. *Position of the Heart*[1]

Kaushiva (1940) points out that he was the first person to note the asymmetric position of the heart and the elongation of the anterior arteries of the left side in the Indian turtle *Lissemys punctata*, but Ahsan Al-Islam & Iftikhar Hamid (1951) gave the credit of this recording to Dhillon (1938), but did not cite the literature. According to Mathur (1946) such a displacement and tilting is probably due to the retractility of the neck into the antero-medial part of the trunk. Ahsan-Al-Islam & Iftikhar Hamid (1951) disagree with Mathur's explanation on the ground that in the common turtle (not named) " whose neck is notoriously contractile ", the heart and anterior blood vessels were perfectly symmetrical. They do not offer an alternative explanation but state that this can be proved only by a study of development and by comparative anatomy of different types of turtles and tortoises.

[1] It is important to emphasize here that this work would not have been satisfactorily done if not for the specimens provided by the British Museum (Natural History) London. Representatives of the family Trionychidae are scattered over vast areas of Temperate and Tropical waters. No worker can possibly collect enough species to study a family characteristic. The Museum provided these as well as a well-equipped laboratory, a rich library and on top of all a nice and friendly atmosphere.

It has been shown in this work that the peculiar asymmetric position and tilting of the heart are found in all genera of the family Trionychidae and should, therefore, be considered a general characteristic of the family.

Retractility of the neck could not be the only reason for the displacement of the heart as suggested by Mathur (1946). It is well known that all the subclass Cryptodira, with the exception of the one family Trionychidae, possesses both contractile necks and symmetrical hearts. It seems reasonable to assume that the shifting of the heart is due to two combined factors—the absence of either of which would result in a symmetrical heart. These factors are :

(1) The retractility of the neck which necessitates the presence of bulky muscular tissue at the mid-longitudinal axis of the body.

(2) The reduction of the dorso-ventral axis of the body at the sagittal plane, the carapace being flat or slightly convex, and as near the plastron as possible. The animal is thus provided with a streamlined body which is essential for a good swimmer. The medial part of the body-cavity would not have enough room for both muscle and heart, and the latter has to find accommodation somewhere else. The choice is very limited since the cavity on the left side of the base of the neck is occupied by a dilated portion of the oesophagus and the only possibility is at the right side of the base of the neck.

The following examples show that the two factors combined are necessary for the shifting of the heart :

(a) *Testudo graeca* Thomson (1932). The neck is quite retractile. The missing factor is the carapace which is dome-shaped and forms a high roof at the medial part of the body. The heart here is perfectly symmetrical.

(b) *Chelys fimbriata* (B.M. 97.5.15.1, from Trinidad). A freshwater turtle with a carapace slightly convex and a dorso-ventral diameter comparable to that of *Trionyx*. The missing factor is the neck, which is not retractile. Dissection of the specimen showed a symmetrical heart.

To emphasize the above-mentioned theory, it has been shown that in *Cyclanorbis*—the only *Trionychid* with a comparatively more convex carapace—the heart lies nearer to the sagittal axis of the body, which actually passes through the left auricle.

Explanation of the tilting of the heart has not been attempted before. It occurs later in life since the new hatches examined had the mid-longitudinal axis of the heart parallel to that of the body. Owing to the position of the heart at the right side, arteries running to the left side of the body extent horizontally ventral to the base of the neck, while those of the right side proceed roughly in an anterior direction (Text-fig. 1). It is quite possible that the rapid growth of the muscles at the base of the neck exert a pushing pressure on the left arteries, and the latter in their turn would pull at the antero-left side of the ventricle where they are attached and cause the tilting. The right side arteries extend anteriorly and are not in a position to give an opposite and equal pulling pressure to stop such tilting.

2. *Structure of the Heart*

The division of the cavum grandum (dorsale) into a cavum sinistrum and a cavum dextrum by a complete partition in the posterior part of the ventricle, as stated by

Mathur (1946) in *Lissemys punctata*, agrees with the condition as found in *C. oligotylus*, but is different from that in *T. triunguis*, where the septum is too short to form an effective partition.

O'Donoghue (1918) divides the ventricle into a right ventro-lateral " cavum venosum ", and a left dorso-lateral " cavum arteriosum ", with an almost entirely separate division of the former, " the cavum pulmonale ". Goodrich (1919) and other authors use the same terms but consider them as three, and not two cavities. It was considered preferable to use descriptive terms for naming the cavities, as was done by Foxon (1955), rather than using terms based on their supposed function. The term " cavum pulmonale " used by Huxley (1871) is appropriate because the cavity is closely associated with the pulmonary artery. Huxley (1871) makes the main division of the ventricle that by the auriculo-ventricular valve into cavum venosum and cavum arteriosum. Parker & Haswell (Sixth edition, pp. 413–414), likewise divide " the left-hand portion which is much the larger " imperfectly into the cavum arteriosum on the left and the cavum venosum on the right, " by the two elongated flaps of the auriculo-ventricular valve, which project freely into the cavity of the ventricle ". This division could not be justified as it is obvious that during ventricular systole, the flaps of the valve are pushed forwards and adhere to the auriculo-ventricular openings, and the supposed cavities disappear.

Division of the ventricle according to the incomplete inter-ventricular septum is the only reasonable basis for division. The two cavities resulting are not comparable in size. The terms " cavum magnum " and " cavum parvum " instead of " dorsale " and " ventrale " or " pulmonale " would probably give a more accurate description of these cavities which are in fact neither quite dorsal nor quite ventral.

Thomson (1932) states that the inter-ventricular septum is, to some extent, continuous with the inter-auricular septum. This is definitely not the case in the two species examined by the author, where there is no continuity or relationship between the two septa.

Goodrich (1916 : 271) says that the inter-ventricular septum *in reptiles* divide the chamber into a left cavity leading to the base of the right systemic arch, and a right cavity leading not only to the base of the pulmonary but also to that of the left systemic arch. It is probably better not to generalize reptilian hearts where we have three different types in Lizards, Chelonians, and Crocodiles with major differences between them. As far as Chelonians are concerned, the bases of the pulmonary and left systemic arches do not belong to the same cavity. During systole, the ventricular wall is drawn into the free edge of the inter-ventricular septum blocking the cavum parvum (pulmonale) and pulmonary arch entirely from the rest of the ventricle, but the base of the left systemic lies outside the septum and it draws blood from the main large cavity. Again, the latter cavity does not lead to the base of the right systemic arch alone as in the above statement but also to the base of the left systemic. Karandikar & Kashyap (1956) describe a generalized reptilian heart which differs in shape and in the openings of the arteries from the Chelonian heart.

Ewer (1950) puts forward the view that the left systemic in reptiles persists as a mechanical necessity—a safety valve to take away into the systemic circulation blood which could not be accommodated in the vessels of the lungs. This explanation would assume that the greater part of the blood conveyed in this vessel is deoxygenated.

The diagram of Goodrich (1919) illustrating Chelonia, Lepidosauria and Rhyncocephalia is rather misleading for the Chelonia because :

(*a*) It shows the two auricles opening in both cavities of the ventricle, while actually they open into one (the magnum, dorsale or left cavity).

(*b*) The incomplete inter-ventricular septum is shown as an extension of the inter-auricular septum, which is not the case.

(*c*) The pulmonary does not come out of a special compartment of the ventricle.

Goodrich (1919) also states that " whereas in the Chelonia, as in the Crocodilia, the left arch receives most of its blood from the cavum pulmonale, in the Lacertilia and Ophidia it opens more dorsally so as to receive arterial blood as well ". The writer agrees that the opening is situated in a region of the ventricle which contains deoxygenated blood, but it is not cut off from the main cavity with its mixed and oxygenated blood. It is so close to the opening of the right systemic, although slightly ventral and more to the right, that it inevitably receives some oxygenated blood. This view was confirmed by estimation of the percentage of oxygen saturation in blood samples taken from the right and left systemic arches, the pulmonary artery and the two auricles (Table I).

Von Hofsten (1941) emphasized the importance of the origin of the left systemic arch in relation to the ventricular septum. Whether this arch receives blood from one ventricle or the other, or even a mixture from both, would depend on this relationship. His diagram for the Chelonian type of heart shows the pulmonary and left systemic arches originating from one chamber, which is not strictly correct. The inter-ventricular septum is shown sloping towards the left side instead of the right, and its free margin should be opposite the right and not the left wall, so that blood would pass dorsal to the septum and around its free border into the right (parvum or pulmonale) portion of the ventricle.

From the evolutionary point of view, possibly the Chelonian heart may be an end line in itself which could not have led into the four-chambered avian heart. As Foxon (1955) states, " the completion of the ventricular septum must be achieved not only so that the arterial and venous blood are distributed to the correct arteries, but also so that the left and right divisions of the auricle open into the corresponding ventricle ". There are two possible ways for the complete division of the ventricle in the Chelonian heart :

(*a*) If the inter-ventricular septum extended to the opposite wall, then both auricles would open into one ventricular cavity (the magnum, dorsale or left) and circulation would not be possible.

(*b*) If the secondary septum developed as suggested by Goodrich (1919), " by the growth from behind forwards of a new muscular septum differentiated from the muscular strands which unite the base of the old septum with the dorsal wall of the ventricle ", then the openings of the arterial arches would all be on one side (the right ventricle), and again circulation would not be possible.

There is still the possibility that simultaneously with the development of Goodrich's secondary septum, the right systemic may have changed its position and extended to the left of the new septum. An avian four-chambered heart would thus be developed.

3. *Experimental*

The short experimental part added to find out whether the heart circulation—as predicted by a study of the heart beat, the ventricular cavities and the relation of the arterial arches to the latter—was correct or otherwise, gave some interesting results.

Broadly speaking it may be said that it confirms the well-known and accepted theory that oxygen-saturation is higher in the *right systemic* artery than in the *left*, and in the latter than in the *pulmonary*. It is worth noting that the *pulmonary arch* contains a slightly higher oxygen-saturation than the right auricle, thus some slight mixing takes place in the ventricular cavities during passage of the blood from the right auricle to the *pulmonary arch* as shown by Steggerda & Essex (1957).

Again oxygen-saturation in the *right systemic arch* is only slightly lower than in the left auricle, which shows that in spite of the incomplete division of the ventricle into two chambers, the system is quite efficient in providing the head with highly oxygenated blood. Even in species where a *ductus arteriosus* connects the pulmonary artery on either side with the corresponding systemic artery—Bojanus (1819–21), O'Donoghue (1917) and Mathur (1946)—the ductus arteriosus opens a long way beyond the exit of the *innominate* artery which supplies the anterior arteries.

It is important to record that an open " *ductus arteriosus* " is not a constant feature of turtles. It was found as a vestige of connective tissue by Thomson (1932) in *Testudo*, and by Girgis (1960) in *Trionyx*. An open *ductus arteriosus* would cause mixing of the venous blood with that of the right and left systemics. It is therefore of great importance to note the presence or otherwise of an " open " *ductus arteriosus* in any Chelonian when the question of oxygen saturation in the two systemics is dealt with. It would be interesting to know whether *Chelydra serpentina* possess an " open " *ductus arteriosus* or not as this would throw some light on the oxygen saturation in the two aortae given by Steggerda & Essex (1957).

SUMMARY

1. In the Trionychidae the heart lies at the anterior right part of the abdominal cavity. It is tilted so that its mid-longitudinal axis forms an acute angle with the mid-longitudinal axis of the body.

2. As a result of the situation of the heart, the left anterior arteries and veins are considerably longer than the right.

3. The asymmetrical position of the heart is shown to be a general characteristic of the family Trionychidae and it may have resulted from the retractility of the neck, combined with shortness of the dorso-ventral axis to facilitate swimming. In *C. oligotylus* where the carapace is more convex, the heart lies nearer to the sagittal axis.

4. The sinus venosus lies outside the pericardium on the dorsal side.

5. The right auricle is larger than the left, and both auricles open on the left side

of the ventricle. The openings are guarded by valves which help to direct the course of the blood within the ventricle.

6. The ventricle is incompletely divided by an oblique septum into a dorso-lateral "cavum magnum" and a ventro-lateral "cavum parvum". The cavum magnum is divided at its posterior part by a secondary septum into left and right cavities. The secondary septum is prominent in *Cyclanorbis oligotylus*, and short and insignificant in *Trionyx triunguis*.

7. The opening of the common pulmonary arch lies in the cavum parvum, that of the left systemic arch in the antero-ventral wall outside the cavum parvum, and that of the right systemic arch in the dorsal wall, anterior and slightly medial to the opening of the left systemic.

8. The pulmonary arch receives deoxygenated blood, the left systemic arch mixed blood and the right systemic oxygenated blood.

9. The arterial arches and their branches are followed until they have passed through the pericardium.

10. The veins entering the sinus venosus and the left auricle are described.

11. Coronary arteries and veins are described.

12. A description of the beating of the heart and the double circulation is given.

13. The hearts of *Trionyx triunguis* and *Cyclanorbis oligotylus* are compared.

14. Analysis of samples of blood in the three arches and in the two auricles confirm anatomical findings.

15. A general discussion follows.

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